DEPTH DEPENDENT MORPHOLOGICAL VARIATION IN TWO OPHIDIIFORM FISHES FROM THE DEEP RED SEA: EVIDENCE FOR SPECIES-SPECIFIC STRUCTURE IN VERTICAL DISTRIBUTION*

by

Franz UIBLEIN (1, 3), Jørgen G. NIELSEN (2) and Wolfgang KLAUSEWITZ (1)

ABSTRACT. - Data on depth distribution and morphology of two ophidiiform fishes from the Red Sea, *Oligopus robustus* (Smith & Radcliffe, 1913) and *Neobythites stefanovi* Nielsen & Uiblein, 1993, were examined for possible species-specific relationships between depth, size, and important morphological variables. In the Red Sea, both species have colonized greater depths than in the Indian Ocean, a pattern most likely related to the higher temperatures in the deep Red Sea. In contrast to *N. stefanovi, O. robustus* occupies a wider depth-range (434-804 vs. 363-1258 m) living in habitats with and without solar illumination. Significant negative correlations between depth and orbit length and two measures of mouth size were found in specimens of *O. robustus* reflecting a high phenotypic plasticity. This morphological plasticity may be associated with a less visually oriented lifestyle in depths of more than 1000 m and probably with a highly size-selective foraging mode in shallower habitats. In *N. stefanovi*, depth was negatively correlated with standard length indicating an upwards directed, ontogenetic migration which coincides well with the development of an ocellus on the dorsal fin that may allow to adapt to increased predation pressure. The species- specific and ecophenotypic approach used in the current study provides a useful tool to determine the rules guiding the depth distribution of deep-sea fishes.

RÉSUMÉ. - Contrairement à la conception traditionnelle admettant que la distribution bathymétrique des poissons de profondeur suivent des règles générales, nous utilisons une approche différente qui essaie de déterminer les relations "espèces-spécifiques" entre la profondeur de vie et les caractères morphologiques et environnementaux importants chez deux espèces d'ophidiiformes récemment découvertes en Mer Rouge, *Oligopus robustus* (Smith & Radcliffe, 1913) et *Neobythites stefanovi* Nielsen & Uiblein, 1993. En Mer Rouge, ces deux espèces ont colonisé des profondeurs plus grandes que dans l'Océan Indien, cette distribution résultant probablement des températures plus élevées des eaux profondes de la Mer Rouge. Contrairement à *N. stefanovi, O. robustus* occupe une gamme plus étendue de profondeurs (434-804 vs. 363-1258 m), vivant à la fois en zone illuminée et en zone obscure. Des corrélations négatives significatives ont été trouvées entre la profondeur, la longueur de l'orbite et deux dimensions de la bouche chez des spécimens d'*Oligopus robustus* provenant de plus de 1000 m de profondeur, reflétant une grande plasticité de la forme du corps et probablement un changement du mode de nutrition résultant de l'absence de lumière à ces profondeurs. Chez *N. stefanovi*, la profondeur était corrélée négativement avec la longueur standard indiquant une migration ontogénétique dirigée vers le haut qui coïncide bien avec le développement d'un ocelle sur la dorsale pouvant permettre de faire face à l'augmentation de la pression de prédation. Notre approche "espèce-spécifique" fournit un outil utile pour déterminer les règles régissant les distributions bathymétriques des poissons de profondeur.

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(1) Forschungsinstitut Senckenberg, Senckenberganlage 25, D- 60325 Frankfurt a.M., GERMANY.
(2) Zoologisk Museum, Universitetsparken 15, DK-2100 Copenhagen, DENMARK.
(3) Present address: Konrad Lorenz-Institut für Vergleichende Verhaltensforschung, ÖAW, Savoyenstrasse 1a, A-1160 Vienna, AUSTRIA.

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Fishes of the order Ophidiiformes occur in marine, estuarine, and freshwater habitats, in tropical reef areas, on the continental shelf, in the abyssal and pelagial of the oceans, as well as in caves (Cohen and Nielsen, 1978). In response to the particular ecological conditions of the different habitats, these fishes have evolved a high degree of intergeneric and interspecific variability in morphological traits including the sensory organs (Gosline, 1968). For instance, the ophidiid genus *Neobythites* occurs almost exclusively in depths of less than 1000 m and shows well developed, large eyes (Marshall, 1954; Nielsen, unpub. data). The genera *Abyssobrotula*, *Sciadonus*, and *Lucifuga*, however, dwell in abyssal depths of several 1000 m or in freshwater caves and have reduced eyes (Munk, 1966; Cohen and Nielsen, 1978; Wilkens, 1986). Even in the clearest oceanic water, solar illumination penetrates to less than 1000 m depth and only bioluminescence may account for the fish eyes to be functional in deeper habitats.

Ophidiiform fishes may also show a high degree of intraspecific morphological variability related to the colonization of new habitats. In a recent comparative study on populations of the bythitid species *Oligopus robustus* (Smith & Radcliffe, 1913) from the Red Sea and the Gulf of Aden, Klausewitz and Uiblein (1994) found that the Red Sea specimens are distributed from 363 m to 1258 m depth. This species shows a high morphological variability among geographically and bathymetrically separable groups with individuals from more than 1000 m depth having particularly small eyes and short pectoral fins.

Another ophidiiform species of the Red Sea, *Neobythites stefanovi* Nielsen & Uiblein, 1993, has been found only in depths of less than 804 m and may be more bound to habitats illuminated by sunlight. Besides its large eyes, *N. stefanovi* has an ocellus placed on the dorsal fin. The ocellus may serve either to deter or to repel visually hunting predators, or to misdirect their attacks towards less vital parts of the body as in several other fishes (Neudecker, 1989; Winemiller, 1990; Meadows, 1993), and should thus have functional value only in well illuminated habitats.

Only a few studies on depth distribution patterns of deep-sea fishes have put the emphasis on a detailed consideration of the biology of individual species and the prevailing ecological conditions in the respective study area (e.g., Carney *et al.*, 1983; Haedrich and Merrett, 1990). More recently, Stefanescu *et al.* (1992) found that depth-size trends in Mediterranean deep-sea fishes show species-specific rather than generally applicable patterns. In the present study, we further advance this approach trying to detect species-specific relationships between depth, size, and intraspecific morphological variation in *Oligopus robustus* and *Neobythites stefanovi* of the Red Sea.

MATERIAL AND METHODS

A detailed description of the specimens examined and the methods of measurements used in the current study is given by Klausewitz and Uiblein (1994) for *Oligopus robustus*, and by Nielsen and Uiblein (1993) for *Neobythites stefanovi*. The material consists of 18 specimens of *O. robustus*, standard length (SL) 33-122 mm, from depths between 363 and 1258 m, and 21 specimens of *N. stefanovi*, SL 29-122 mm, from depths between 434 and 804 m, all originating from the northern and central region of the Red Sea between 26° 39'N and 18° 35'N. All specimens were caught by benthic trawls during the three MESEDA expeditions 1977-1981 and the METEOR V expedition 1987 and are deposited and catalogued at the Research Institute and Natural History Museum Senckenberg at Frankfurt/M., Germany. The MESEDA expeditions used a closing trawl (Thiel, 1980), while the METEOR V expedition used a beam trawl (Türkay, 1987). Both trawls were equipped with fine-meshed cod ends, minimum mesh size 8-10 mm. Of 54 total trawls nine contained *N. stefanovi*, seven *O. robustus*, and one both species (Fig. 1).

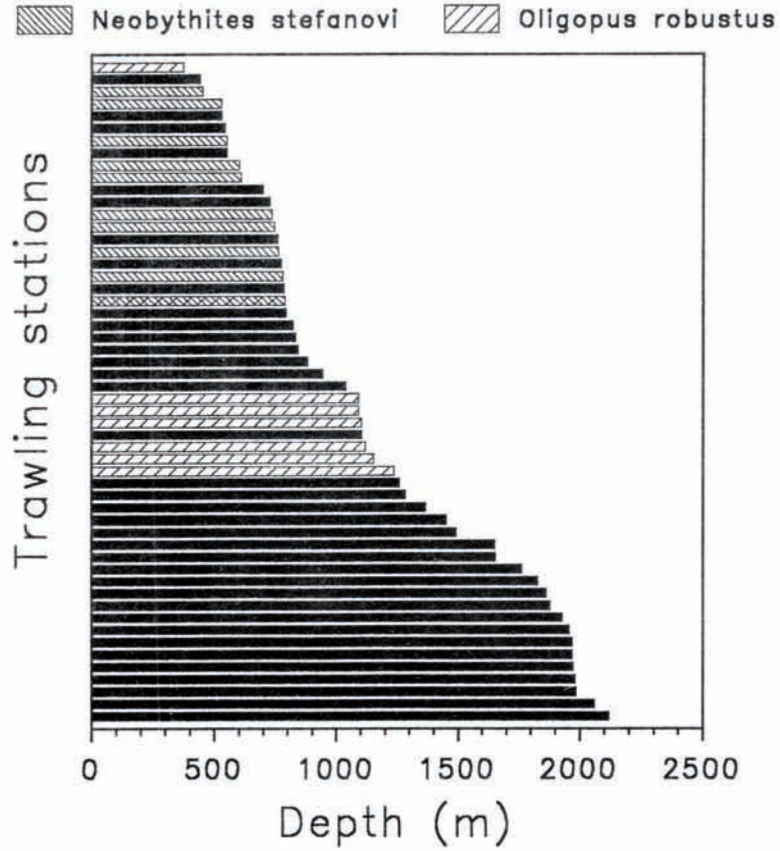

Fig. 1. - Mid-depth distribution of the 54 trawling stations in the Red Sea during three MESEDA expeditions 1977-1981 and the METEOR V expedition 1987. Trawl-hauls containing specimens of *Oligopus robustus* or *Neobythites stefanovi* are highlighted.

For the statistical analysis, the mid-depth of each trawling station was calculated from the depth ranges covered by the respective trawl. Standard length and orbit length were obtained from both species. In *Oligopus robustus*, the following measurements were also analysed: head length, snout length, interorbital length, upper jaw length, upper jaw width (the distance between the posterior tips of upper jaws), and pectoral fin length. The data were size-adjusted by running log-log regressions between SL and all continuous variables. All regressions showed high correlation coefficients (r > 0.95) and were highly significant

Table I. - Ocellus developmental stages in *Neobythites stefanovi* (for further explanations see text).

Stage	Spot	Ring
1	absent	absent
2	lightbrown	absent
3	brown	absent
4	brown	anterior, posterior
5	darkbrown	anterior, posterior
6	darkbrown	almost complete
7	blackish	almost complete
8	black	complete

($p < 0.0001$). The adjusted measurement of each variable expressed as the individual deviation (residual) from the regression function (Reist, 1985; Uiblein and Winkler, 1993) was used in the subsequent analysis.

To determine the degree of ocellus development in *N. stefanovi*, eight stages were defined based on the present material and additional specimens from the Gulf of Aden (see also Nielsen and Uiblein, 1993). The stages could be distinguished according to the presence and pigmentation of a spot, the presence of a ring, and the degree of ring formation around the spot (Table I).

To examine the relationship between depth distribution and the morphological measurements obtained from each individual of the two species, Spearman's rank correlation method was employed (Fowler and Cohen, 1990).

RESULTS

Oligopus robustus

In *Oligopus robustus*, no significant correlation was found between depth and SL ($r = 0.02$, $p > 0.05$; Fig. 2a). However, a highly significant negative correlation occurred between depth and orbit length ($r = -0.80$, $p = 0.001$) with all specimens from more than 1000 m depth showing smaller values than their conspecifics from shallower water (Fig. 2b). Similar to orbit length, a highly significant negative correlation was found between depth and upper jaw width ($r = -0.71$, $p < 0.005$) with a clear separation between specimens from more than 1000 m depth and all others (Fig. 2c). A weaker, but still significant negative correlation with depth occurred in pectoral length ($r = -0.64$, $p < 0.025$) and in upper jaw length ($r = -0.50$, $p < 0.05$). All other variables examined were not significantly correlated with depth.

Neobythites stefanovi

In *Neobythites stefanovi*, a highly significant negative correlation was found between depth and SL ($r = -0.74$, $p < 0.001$; Fig. 3a). In contrast to *O. robustus*, this species showed no significant correlation between depth and orbit length ($r = -0.11$, $p > 0.05$; Fig. 3b).

The eight different stages of ocellus development (Table I; Fig. 4 shows stages 2, 4, 6, and 8) were strongly positively correlated with SL ($r = 0.92$, $p < 0.0001$). As a consequence, depth and ocellus developmentai stage were strongly negatively correlated (r =

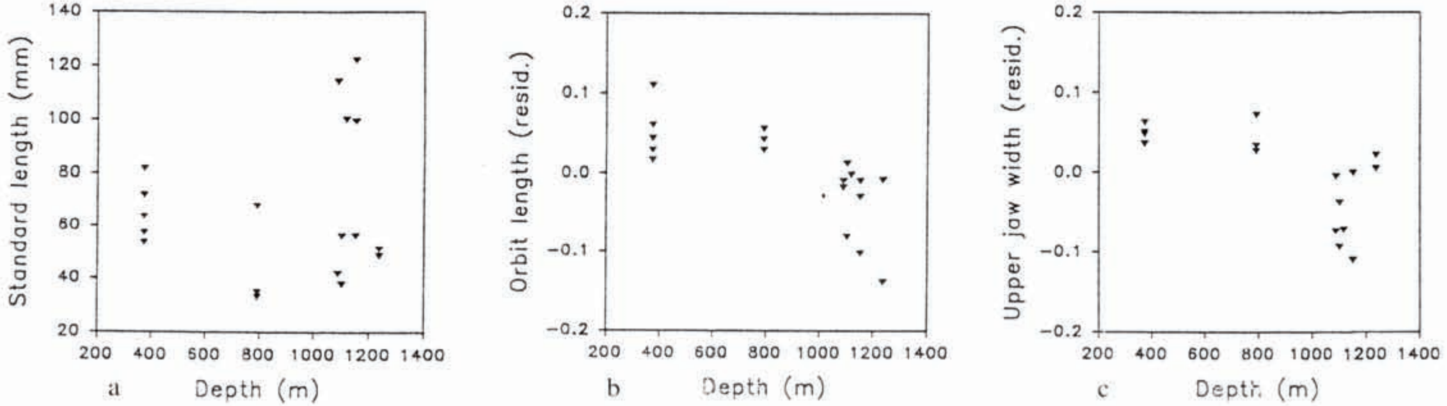

Fig. 2. - a) Depth against SL; b) depth against size-adjusted values (residuals) of orbit length and c) depth against size-adjusted values (residuals) of upper jaw width in *Oligopus robustus*.

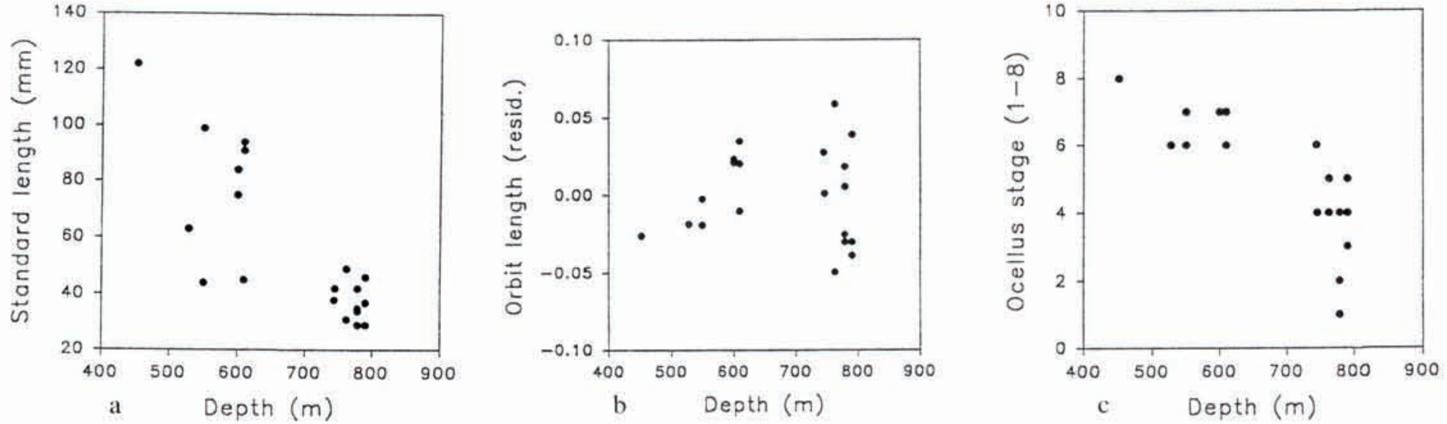

Fig. 3. - a) Depth against SL; b) depth against size-adjusted values (residuals) of orbit length and c) depth against ocellus developmental stages in *Neobythites stefanovi*.

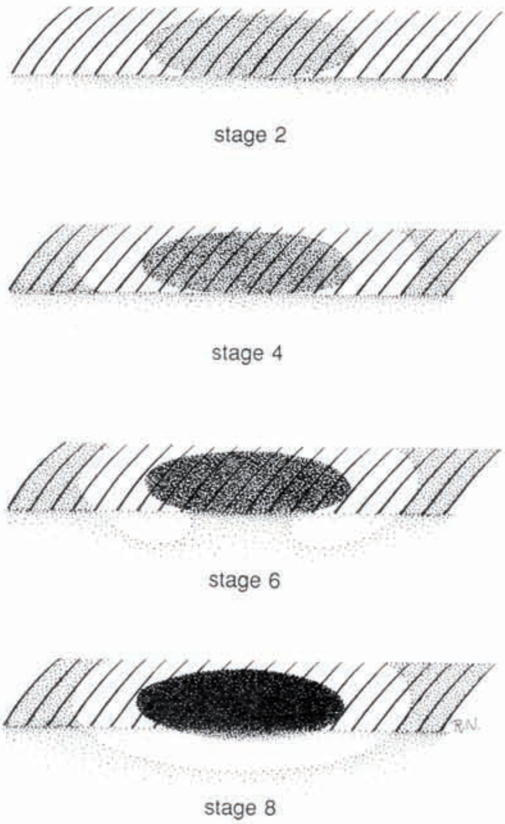

Fig. 4. - Scheme of ocellus developmental stages 2, 4, 6, and 8 in *N. stefanovi* (see also Table I).

-0.81, $p < 0.001$; Fig. 3c). Specimens with ocellus stages between one and five (all with a SL of less than about 50 mm) were caught only in depths of more than 720 m. Specimens with SL of more than about 50 mm all had a well developed ocellus (stages six to eight) and were collected in depths ranging from 609 m upwards to 451 m.

DISCUSSION

In the Red Sea, *Oligopus robustus* and *Neobythites stefanovi* occur at greater depths (363-1258 vs. 434-804 m) than in the adjacent parts of the Indian Ocean (Klausewitz and Uiblein, 1994; Nielsen and Uiblein, 1993). These regional differences in depth distribution have to be seen with special regard to the particular conditions in the Red Sea with temperatures of about 21.5° C vertically throughout the water body. The consistently high tem-peratures may allow fishes from shallow warm-water habitats to enter greater depths which might be inaccessible in other seas due to much lower temperatures.

Oligopus robustus shows a particularly broad depth range extending from well illuminated zones into levels only illuminated from bioluminiscence at 1000 m and deeper. Interestingly, the depth distribution of *O. robustus* is discontinuous, with probably three separated populations, one in depths of about 350 m, one in about 750 m, and a third one in about 1200 m depth (Fig. 1, see also Klausewitz and Uiblein, 1994). The sampling gaps are unlikely to be artifical, because a large number of trawl-hauls covered the whole depth range of *O. robustus*. Moreover, several trawl-hauls succeeded to catch *N. stefanovi* in depths between 400 and 700 m (Fig. 1).

While *Neobythites stefanovi* remains within the solar illuminated zone, *Oligopus robustus* has also colonized the real deep-sea environment of some 1000 m and deeper and may - like many secondary deep-sea fishes (see Rass, 1966, and citations therein) or facultative cave dwellers (Uiblein *et al.*, 1992) - have an excellent capability of adapting both to well illuminated and to lightless habitats. *O. robustus* has relatively small eyes and a well developed lateral line system, a common feature in the genus *Oligopus* (Cohen, 1964). The closely related species *Oligopus ater* Risso, 1810, also shows affinities to enter lightless environments: individuals of this species have been found to live and most probably reproduce in deep submarine caves in the littoral zone of Mallorca island, western Mediterranean (Bori *et al.*, 1985).

The morphological differentiation found in *Oligopus robustus* specimens from depths of more than 1000 m indicates a highly plastic response to the specific environmental conditions in these depths. All of these specimens have smaller eyes which may be related to the adoption of a less visually oriented lifestyle. Specimens of *O. robustus* from the Red Sea have larger mouths and heads than those from the Gulf of Aden (Klausewitz and Uiblein, 1994), and the mouth size is especially large in specimens from shallower depths. If the assumption of a highly size-selective foraging mode in Red Sea specimens holds true (see Klausewitz and Uiblein, 1994), this should concern specimens from shallower depths in particular.

The depth distribution of *Neobythites stefanovi* is more continuous than in *Oligopus robustus*, and, a clear bigger- shallower trend was found. The absence of smaller individuals in shallow depths and of bigger ones in deeper areas suggests an upwards directed ontogenetic migration starting in *N. stefanovi* of about 40 mm SL.

Growth-related habitat shifts during ontogeny have been observed in many fish species (Uiblein, 1991, and citations therein). With increasing body size, food consumption also increases. In deep-sea habitats, shallower depths may provide more food (Thiel, 1983), but also contain a higher number of predators (e.g., Giske and Aksnes, 1992). Consequently, upwards directed migrations during ontogeny should be beneficial only, if predation risk can be kept low at the same time. The assumed start of ontogenetic migration in *Neobythites stefanovi* coincides with the development of an ocellus on the dorsal fin. A well developed ocellus reduces the mortality risk from visually hunting predators (Neudecker, 1989; Meadows, 1993) and thus may allow *N. stefanovi* to adapt to increasing predation risk in shallower habitats.

The present study is to our knowledge the first one that aims at detecting species-specific relationships between depth distribution and ecophenotypic variation in deep-sea fishes. Our approach sheds new light on the problem of what governs vertical habitat selection in the deep-sea, and may allow the constraints on depth distribution of other taxa to be tracked similarly. In addition to the search for possible relationships between depth distribution and morphological variables, detailed field and experimental studies are needed to examine more closely the respective characters for their hypothesized biological function.

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